

DISTRIBUTION PATTERNS OF CERTAIN UMBELLIFERAE¹

By MILDRED E. MATHIAS

Department of Botany, University of California, Los Angeles

In a Miscellany in Honor of Merrit Lyndon Fernald, Woodson (1947) discussed the "Historical Factor" in plant geography. Now almost twenty years later it seems appropriate to continue the discussion in a miscellany in honor of Robert Everard Woodson. For years Woodson was intrigued by the relations of paleogeography to present patterns of distribution and variation, particularly of *Apocynaceae* and *Asclepiadaceae*, and we engaged in many discussions on possible interpretations of Angiosperm distributions.

The Angiosperm family *Umbelliferae* is cosmopolitan primarily in temperate areas where it exhibits many interesting patterns of distribution and variation (Fig. 1, 2, 3, 4). Even though the fossil record for the family is inadequate it may be informative to generalize and speculate on the evolution of some of the present distributional patterns.

The two families *Araliaceae* and *Umbelliferae* are a closely related and natural group probably derived from a pro-araliaceous stock. Baumann's (1946) comparative study of the fruit of the New Caledonia genus *Myodocarpus* (*Araliaceae*) and of the *Umbelliferae* supports this view and indicates that the *Umbelli-*

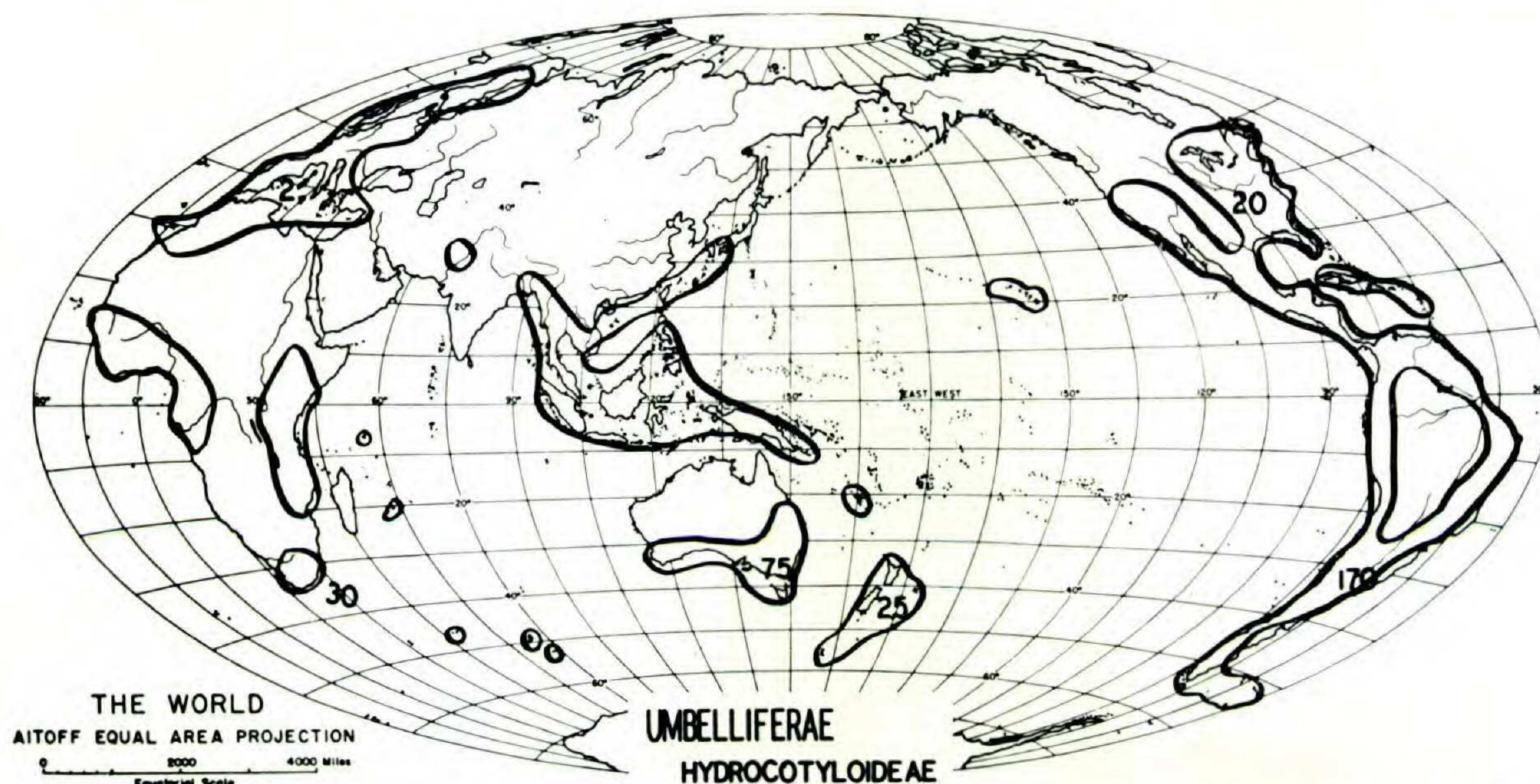


Fig. 1. Distribution of the subfamily *Hydrocotyloideae*, *Umbelliferae* (320 species). Numbers indicate the approximate number of species for each area.

¹ This brief review is a summary of ideas developed over a period of years while conducting taxonomic studies on the American *Umbelliferae* supported by the New York Botanical Garden, the Committee on Research, University of California, Los Angeles, and the National Science Foundation (G-13393 and GB-1293). Many individuals have assisted in the collection of data, preparation of maps, etc. Among them I wish to thank especially Miss Jane Turner, Mr. Allan Andrews, and Mrs. Mimi Lonski, all of the University of California, Los Angeles.

ferae is the more advanced of the two families. The anatomical study of Rodriguez (1957) sustains the thesis that the two families have diverged from a single ancestral source and indicates that, of the tribes of the *Araliaceae*, the *Mackinlayeae* appear to be closest to the *Umbelliferae*. Recent studies by Tseng (1965) on fruit anatomy and pollen morphology present further data to show the probable derivation of the *Araliaceae* and *Umbelliferae* from a common stock.

The modern *Araliaceae* have a wide distribution with a concentration of species in the tropics (Fig. 5). While no taxonomic summaries of the entire family have appeared in recent years those of Harms (1898) and Viguier (1906) give us a general idea of the areas of differentiation and general distribution. Of the some 600 species about 400 occur in tropical areas and only 200 in temperate regions, approximately equally distributed in the northern and southern hemispheres. Harms described three tribes—the *Schefflereae*, in the tropics of all hemispheres with some species extending into temperate regions, one (*Oplopanax horridum*) into western North America; the *Aralieae*, occurring equally in tropical and temperate areas but unknown from Europe and Africa; and the *Mackinlayeae*, all tropical or subtropical in Queensland and New Caledonia. Viguier (1906) recognized ten tribes, all but one of which is represented in the tropics and subtropics of New Guinea, New Caledonia, and eastern Australia.

The *Araliaceae* has long been recognized as an ancient Angiosperm family, and it is well known in the fossil record of the Cretaceous (Axelrod, 1952). About 60 taxa in eight genera have been described from the Cretaceous of North America, some 40 of which have been assigned to the modern genera *Aralia*, *Hedera*, and *Panax*. The tribe *Schefflereae* is represented in the Tertiary floras of North America with 13 taxa in three genera and the *Aralieae* with 38 taxa in three genera (Table 1). The fossil record indicates that the *Araliaceae* were a component of the tropical Tertiary geofloras (Axelrod, 1952). From the present distributions we may infer a probable origin for the family in the paleotropics where some 200 species now occur in Indo-Malaysia, northeastern Australia, and New Caledonia. It is here that we find *Myodocarpus* and taxa assigned to the *Mackinlayeae*, those which show the closest affinity in fruit and wood anatomy to the *Umbelliferae* and which are probably most closely related to the pro-araliaceous stock. The modern temperate elements of the family represent survivors of subtropical taxa which extended farther north in the Tertiary (Chaney, 1947).

The generalized distribution pattern for the *Umbelliferae* shows a clear relationship to that of the *Araliaceae* but reflects the more temperate requirements of the family. Where species occur in tropical latitudes they are, except for a few weedy representatives, confined to high montane temperate or even subalpine habitat. Three subfamilies have been distinguished by students of the family. The *Hydrocotyloideae* (considered a family by Hylander, 1945) consists of some 320²

² Approximate numbers of species in each subfamily and for areas of the world outside the western hemisphere have been based on compilations largely from Drude (1898) and Willis (1951). It is impossible with the present information on the family to arrive at more than approximations. However it is believed that relative proportions of taxa will not be changed significantly as investigations proceed.

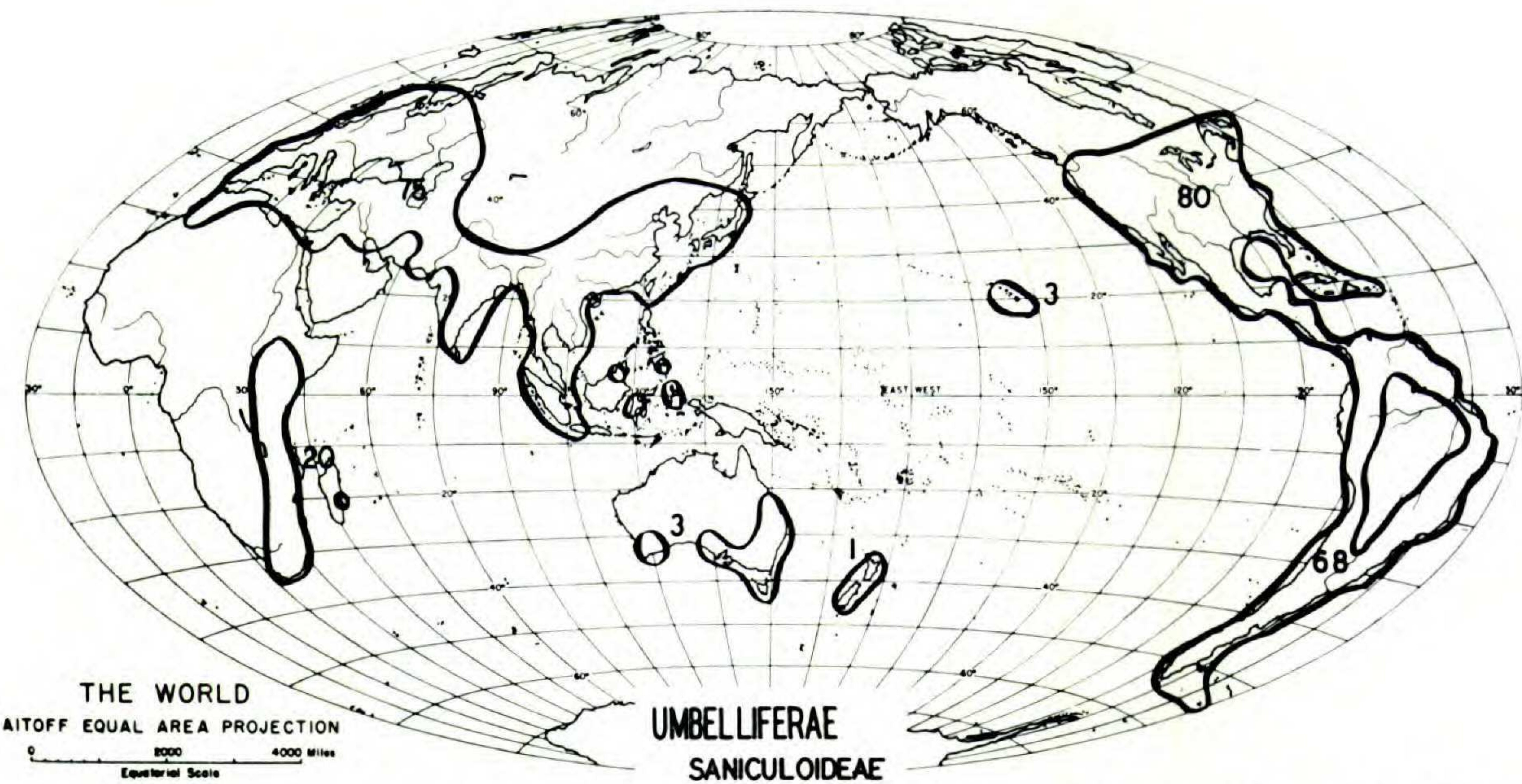


Fig. 2. Distribution of the subfamily *Saniculoideae*, *Umbelliferae* (250 species). Numbers indicate the approximate number of species for each area.

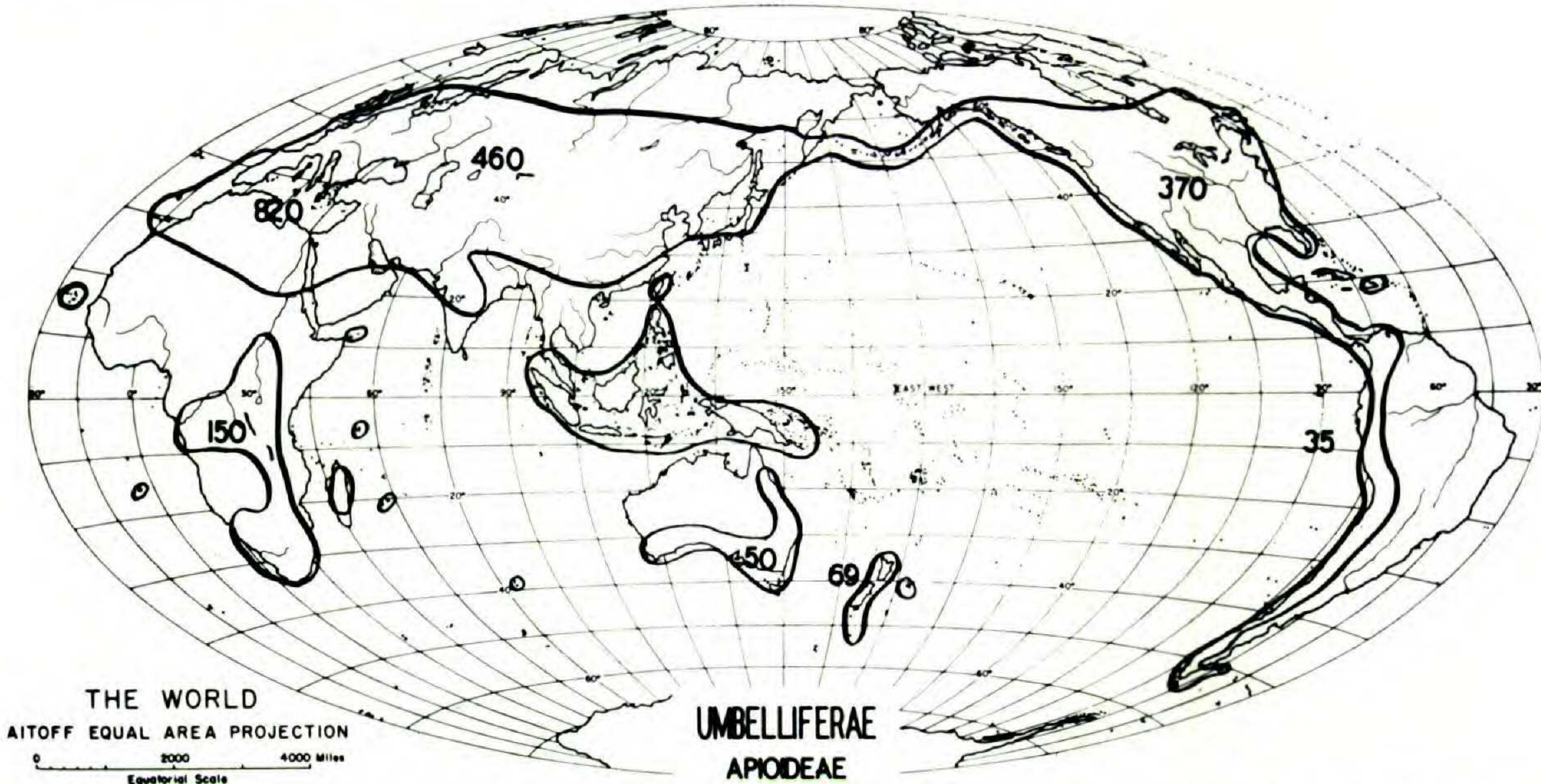


Fig. 3. Distribution of the subfamily *Apioideae*, *Umbelliferae* (1950 species). Numbers indicate the approximate number of species for each area.

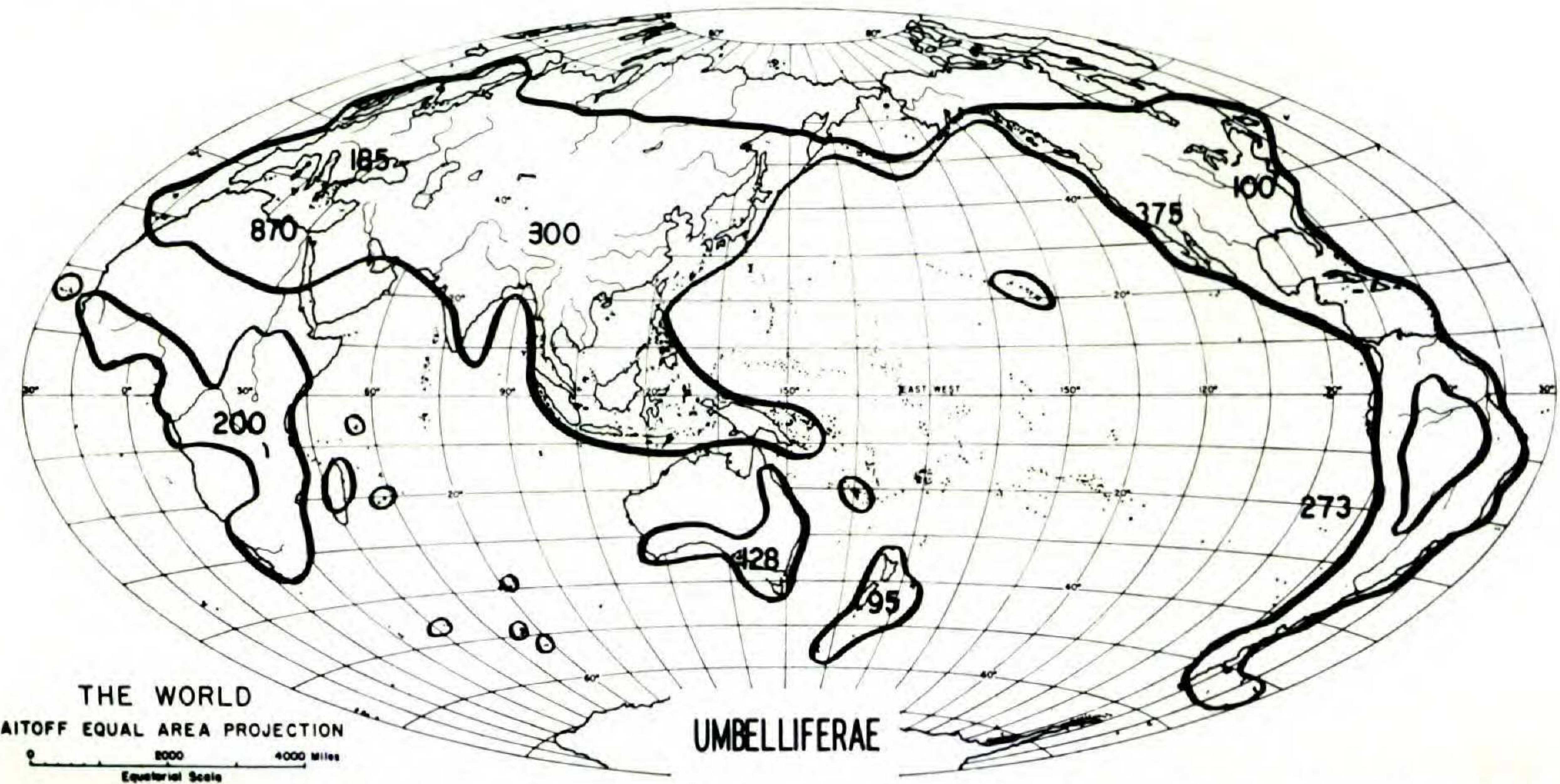


Fig. 4. Areas of differentiation for the *Umbelliferae*. Numbers indicate the approximate number of species for each area.

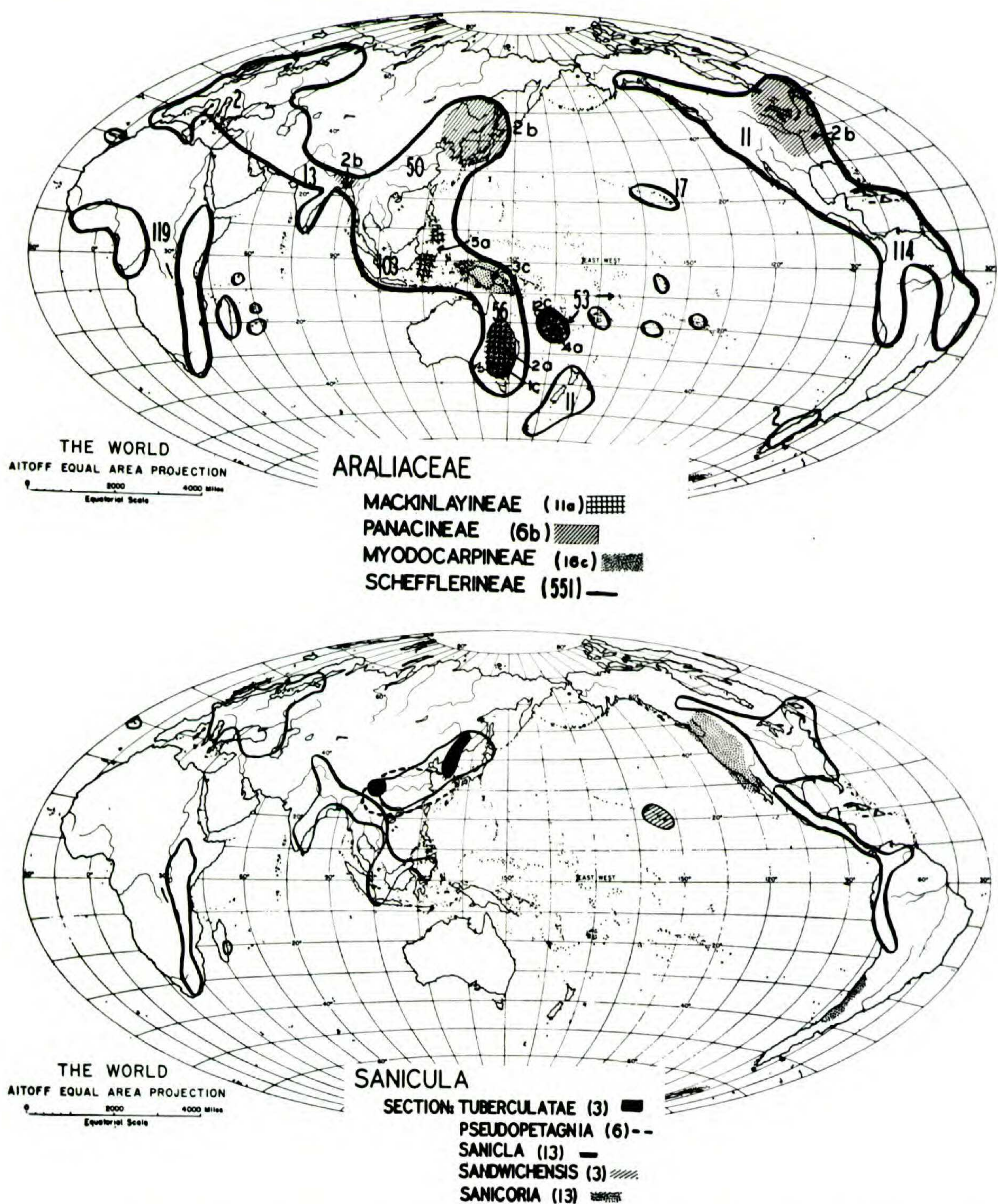


Fig. 5 (top). Distribution of the *Araliaceae* (600 species). Numbers indicate the approximate number of species for each area and have been derived from Harms (1898), Viguiet (1960), and Willis (1951). Fig. 6 (bottom). Distribution of the sections of the genus *Sanicula* (38 species).

species and reaches its maximum differentiation and distribution in the southern hemisphere (Fig. 1). Of the some 30 genera only five have species which range into the northern hemisphere and these are all weedy or aquatic, possibly representing geologically recent invasions. The other two subfamilies, *Saniculoideae* (250 species) and *Apioideae* (1950 species) are bipolar in distribution but reach their maximum development in the northern hemisphere (Fig. 2 & 3). Figure 4 shows two modern centers of differentiation for the family, one in the Mediterranean area

where some 900 species have been recognized and the other in the western United States and Mexico with 375 species. Since the taxonomy of the western North American genera has been under intensive study for several decades this paper will emphasize distribution patterns displayed in this second area of differentiation.

The subfamily *Hydrocotyloideae* is represented in western North America by a limited number of species, most or all of which show southern hemisphere affinities. As indicated above these may represent geologically recent incursions into the flora and consequently have been omitted from this discussion. Continued taxonomic study of the entire subfamily is in progress to clarify both morphological relationships and distributional patterns.

The subfamily *Saniculoideae* is represented in western North America by two genera, *Sanicula* (Fig. 6) and *Eryngium*. The 14 species of *Sanicula* occurring in the Pacific Coast states and Baja California belong to the section *Sanicoria*. Shan & Constance (1951) have described their present distribution and their possible evolution in response to changing climatic conditions since the Tertiary. Raven & Mathias (1960) further discussed the possible evolution of the section *Sanicoria* and concluded that this section apparently stemmed from ancestors adapted to relatively mesic sites within the area of the Arcto-Tertiary Geoflora but occupied successively drier and drier habitats offered by the expansion and differentiation of the Madre-Tertiary Geoflora. Constance (1963) has subsequently commented on the disjunct distribution of two species, *S. crassicaulis* and *S. graveolens*, between Pacific North America and Chile. Only one other species, *S. liberta* of the section *Sanicla*, occurs in western North America, extending from Chihuahua, Mexico to the Andes of Peru and Bolivia. Shan & Constance (1951) believe this species to be a southerly migrant from a widely ranging northern stock.

The genus *Eryngium* presents a much more complex pattern and one for which additional taxonomic and distributional data are needed. The relationship of the taxa of the New and Old World has not been satisfactorily investigated and it is only in recent years that sufficient material has been secured to begin a taxonomic study of the New World taxa. A number of polyploid species are known and Bell (1959) has suggested a correlation between the occurrence of polyploidy and certain distribution patterns. The species which occur in the Pacific Coast states occupy specialized habitats in salt water marshes or pools, freshwater marshes, vernal pools, or seasonally wet meadows.

The largest number of taxa of *Umbelliferae* in western North America belong to the subfamily *Apioideae*. The present distribution of many genera is holarctic and suggestive of a former close affinity with the Arcto-Tertiary Geoflora. This group may be exemplified by the genera *Osmorhiza*, *Sium*, *Ligusticum*, *Heracleum*, *Angelica*, and *Conioselinum*, all of which have representatives in the California flora. Constance & Shan (1948) in their revision of the genus *Osmorhiza* (Fig. 7) called attention to the occurrence of species of the section *Aristatae* in eastern North America and in eastern Asia, a familiar and well-documented pattern indicative of Arcto-Tertiary relationships. Constance (1963) has further commented on the disjunct distributions between Pacific North America and South America for

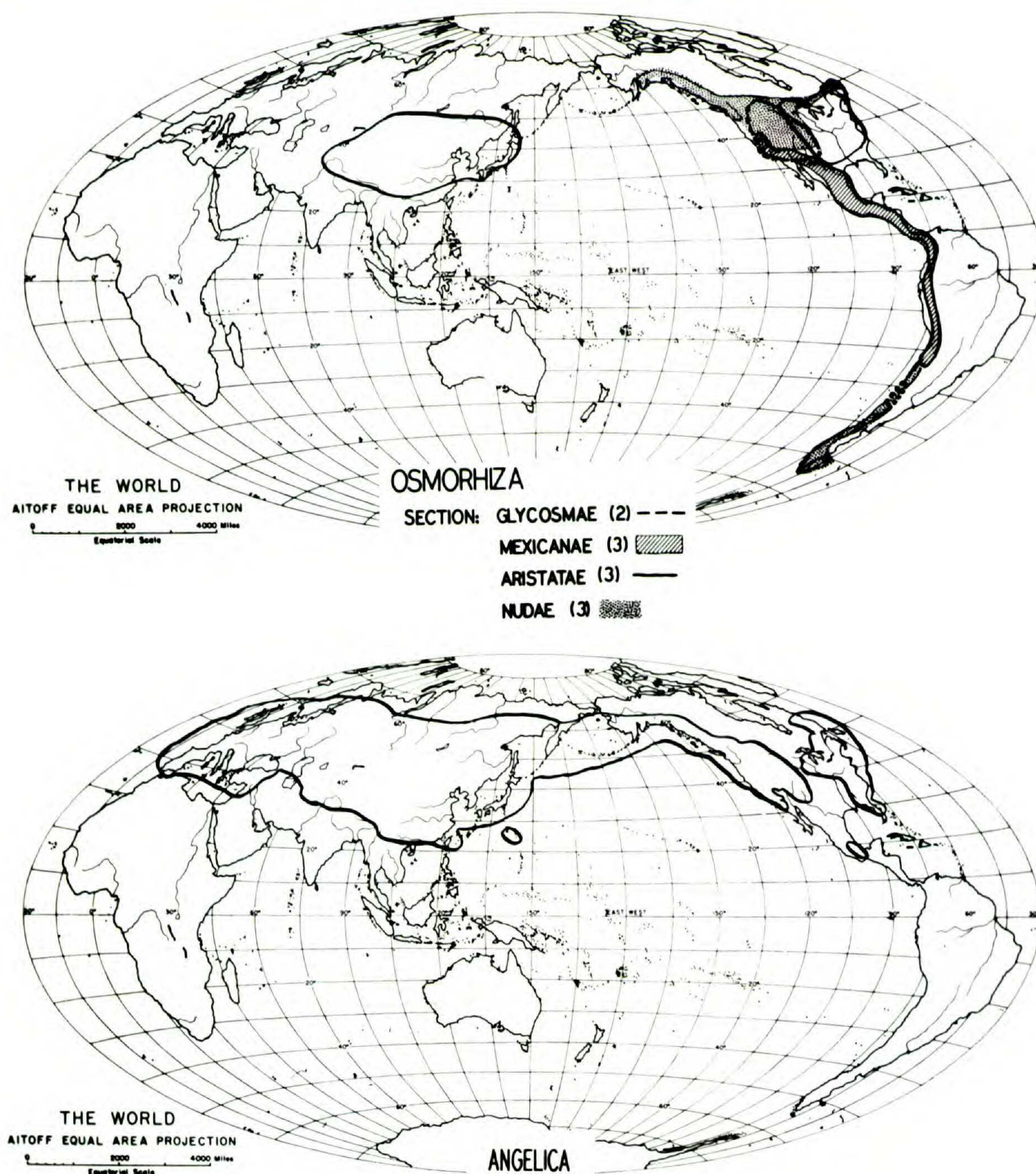


Fig. 7 (top). Distribution of the sections of the genus *Osmorhiza* (11 species). Fig. 8 (bottom). Distribution of the genus *Angelica* (50 species). The five species for New Zealand in H. H. Allan, *Flora of New Zealand*, 1961, have not been included. It is believed that they constitute a distinct genus *Gingidium* (Dawson, John W., *A revision of the genus Anisotome*. Univ. Calif. Publ. Bot. **33**: 6. 1961).

three species, distributions reminiscent of those occurring in *Sanicula*. The genus *Angelica* may be considered typical of the remaining genera listed above. Figure 8 shows its holarctic distribution, the species generally occupying mesic sites often along the margins of forests.

Of special interest are the 39 genera of *Apioideae* with over 200 species which are endemic to western North America. Two centers of distribution may be recognized for these genera; one in Pacific North America, including the Rocky Mountains, where 195 species are endemic, 31 extend into adjacent and equivalent areas,

and only 12 occur extensively in other areas; the second in extratropical Mexico and Central America with 133 endemic species, 23 extending into adjacent and equivalent areas and only two occurring extensively in other areas.

The largest genus in Pacific North America is *Lomatium* with 80 species. A major center for differentiation of this genus (Figure 9A) is in the grass and scrubland of western Washington, Oregon, and adjacent Idaho where over half of the species occur. *Lomatium* is represented in the California flora by 46 taxa, (species and varieties) 10 of which are endemic and show adaptation to such specialized habitats as serpentine outcrops, 19 occur in drier areas of the state associated with sagebrush (*Artemisia tridentata* Nutt.), chaparral, or desert woodland vegetations, and only 17 are in more mesic habitats. Most species of *Lomatium* flower in the early spring before summer drying occurs; they are perennial and may be considered well adapted to the summer dry regime since in drier areas the plants are completely dormant by the beginning of the summer dry season.

The other large endemic genus in Pacific North America, *Cymopterus*, is possibly a derivative of an *Angelica*-like stock which has become adapted to drier sites. Of the 32 species, 28 are found within the Great Basin and desert areas roughly bounded by the Snake River of Idaho, Sierra Nevada of California, Colorado River of Arizona, and the Rocky Mountains of Colorado (Fig. 9B). The species occur in desert areas but cannot be considered true desert plants but rather drought- or desert-evaders. They are deep-rooted perennials and are among the earliest plants to flower in the spring when they may even be found flowering along the edges of snowbanks. The desert species at low elevations occur commonly in sinks or basin areas where water collects seasonally. By early summer they are in mature fruit and the foliage withered. Even at higher elevations their fruiting is completed early in the season. Some years ago I had the opportunity to observe a population of *Cymopterus purpurascens* (Gray) Jones at 7300 feet elevation near the summit of Westgaard Pass, Inyo County, California, in mid-April when young fruit was already forming. On May 30 of the same year it was possible to locate the population only by a few dried leaf fragments and an occasional fruit.

The distribution of the Mexican highland and Central American genera may be exemplified by the genera *Prionosciadium*, *Rhodosciadium*, and *Donnellsmithia* (Fig. 10A) occurring in the mountains from Sonora and Chihuahua to northern Guatemala. Within this general area occur most of the Mexican genera of *Umbelliferae*. However, one fossil record of fruits from the Miocene Latah formation at Spokane, Washington (*Umbelliferospermum latahense*) has been tentatively described as a relative of the modern Mexican genus *Rhodosciadium* (Berry 1929) and is indicative of a much more extensive distribution for this group in the Tertiary. The present distribution of one Mexican highland genus, *Tauschia*, also indicates a wider range in the Tertiary since relict species of the genus occur from coastal Southern California to the northern Cascades in Washington (Fig. 10B). The genus *Arracacia* (Fig. 10C) shows a somewhat different pattern from that of *Prionosciadium* and *Tauschia*, extending for some distance south along the Andean chain and although doubtless of northern affinity and origin it would seem to be advancing into the southern hemisphere. One other taxon may be mentioned, the

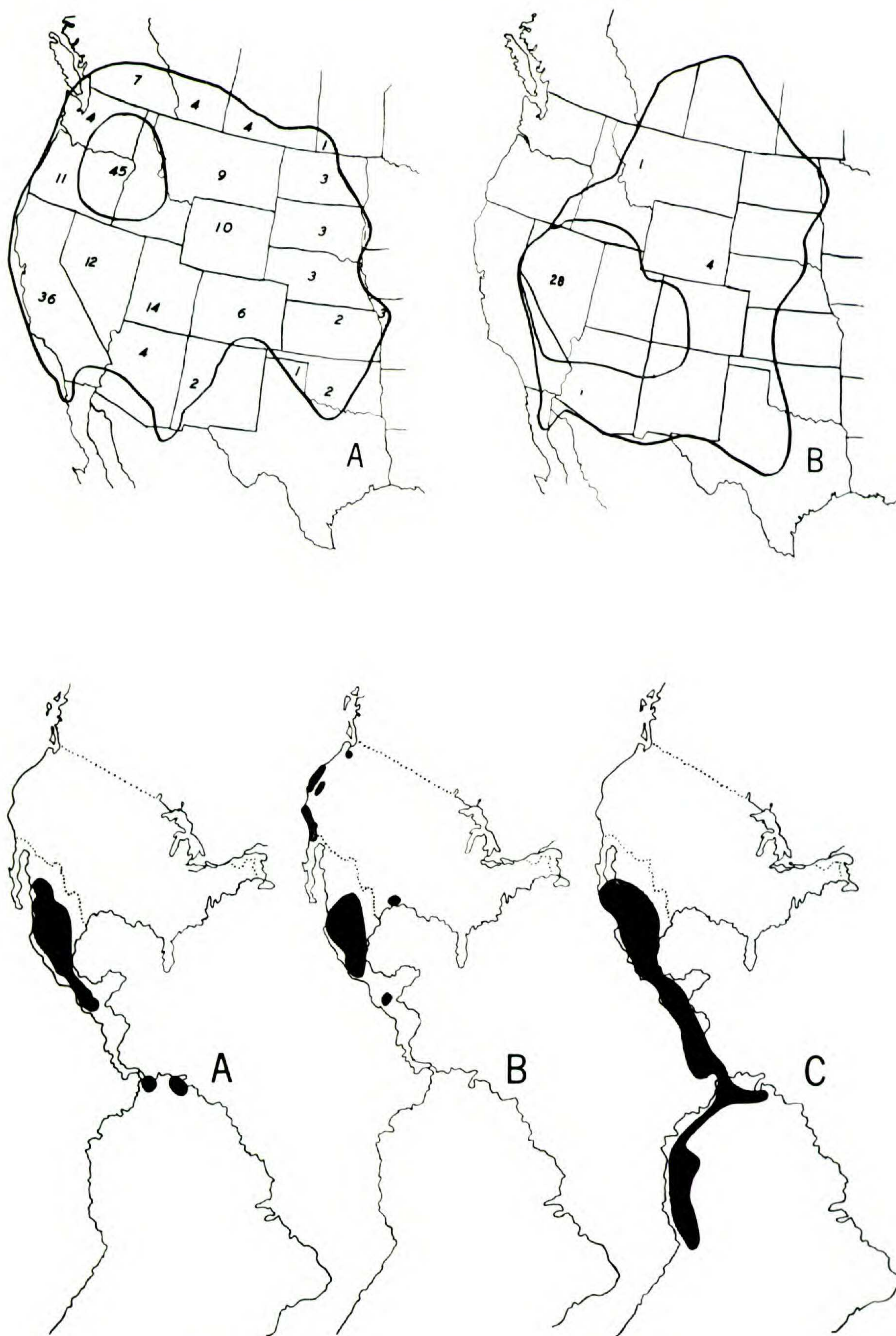


Fig. 9 (top). Distribution of the genera (A) *Lomatium* (80 species) and (B) *Cymopterus* (32 species) in western North America. Numbers indicate the number of species in each general area. Fig. 10 (bottom). Distribution of the genera (A) *Prionosciadium* (16 species), *Rhodosciadium* (13 species), and *Donnellsmithia* (13 species); (B) *Tauschia* (20 species); and *Arracacia* (25 species).

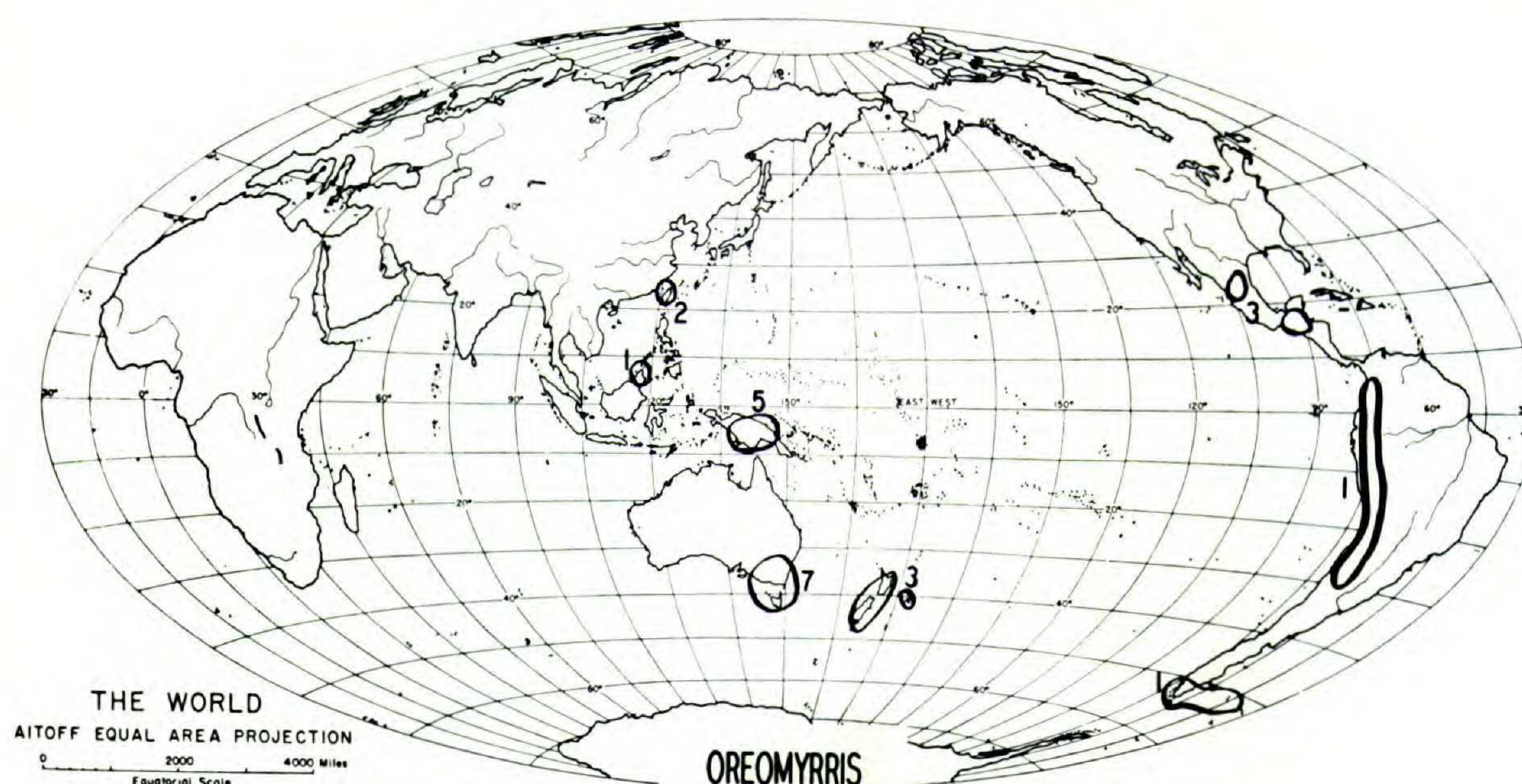


Fig. 11. Distribution of the genus *Oreomyrrhis* (23 species).

genus *Oreomyrrhis* (Fig. 11) which reaches southern Mexico. It is the only member of the subfamily *Apioideae* which occurs almost entirely in the southern hemisphere. Mathias & Constance (1955) have suggested that this genus may be a derivative of an Antarcto-Tertiary Geoflora. Its anomalous distribution is one of many unsolved geographical problems.

It is suggested by these patterns in western North America that with the differentiation of drier climates in the Pliocene certain elements of the widely ranging Umbelliferae became adapted to grasslands and desert borders and were components of the Madro-Tertiary Geoflora. The present Mexican genera may be the modern derivatives of this flora, only the genus *Tauschia* retaining sufficient variability to survive in more northern latitudes. The genera in western North America do not fit into one pattern of distribution but into several. There is still a large representation of Arcto-Tertiary derivatives occurring in mesic habitats, many of the genera essentially holarctic. *Angelica*, *Ligusticum*, *Osmorhiza*, and other genera mentioned earlier are in this category. There is a small group of probable relict genera surviving in mesic montane areas. These include *Podistera*, *Oreonana*, and *Oreoxis*. However the greatest differentiation seems to be occurring in the two groups of genera which became components of the Madro-Tertiary Geoflora, such as *Lomatium* and *Cymopterus* in the Great Basin and the many genera of Mexico and Central America.

The historical development of the family *Umbelliferae* cannot be determined from its fossil record. In North America there are no records prior to the Tertiary and fossil fruits have been described for only seven species in as many genera. Four of these are Pleistocene records referred to modern species (Table 1). Consequently the past history of the family must be inferred largely from a study of modern distributions and their correlation with those for other closely related groups, particularly the *Araliaceae*. It is suggested from this brief survey of the generalized distributions of a few genera of *Umbelliferae* and a comparison of the distribution of the entire family with that of the *Araliaceae* that the *Umbellales*

(sensu strictu) are an ancient tropical group, already differentiated into modern genera or their prototypes in the widely ranging Cretaceous floras of the world. The largely herbaceous *Umbelliferae* were presumably derived from a tropical woody pro-araliaceous stock in temperate environments probably at higher elevations. They expanded both north and south from the tropics and were differentiated, probably by late Cretaceous, into modern sub-families or their prototypes, *Hydrocotyloideae* in the south, *Saniculoideae* and *Apioideae* in the north. The present disjunct distributions for the western hemisphere representatives of the family are the result of climatic and topographic changes beginning in late Oligocene. They are not unique but they may be matched in other families (Axelrod, 1958). Certain of the north-south disjunctions may be the result of recent accidental dispersal or may represent mountain hopping along the Andean chain.

Some Antarcto-Tertiary derivatives of the family have expanded into temperate areas somewhat north of the equator and likewise Arcto-Tertiary derivatives have ranged into the tropics and southward at higher elevations. The primary center of differentiation for the present representatives of the *Umbelliferae* is in the dry climate of the Mediterranean area. A secondary center occurs in western North America. The differentiation and expansion of the family in these regions is apparently in response to progressively drier environments.

Table 1. Cenozoic ARALIACEAE and UMBELLIFERAE of North America¹

	Paleocene	Eocene	Oligocene	Miocene	Pleistocene
ARALIACEAE-ARALIEAE					
1. <i>Aralia alexoensis</i> Bell	Alberta				
2. <i>A. browni</i> Berry		Wyoming			
3. <i>A. browniana</i> Heer	Greenland				
4. <i>A. coloradensis</i> Knowlton	Colorado				
5. <i>A. dakotana</i> Knowlton & Cockerell	British Columbia North Dakota	Mississippi California			
6. <i>A. delicatula</i> Hollick		Alaska			
7. <i>A. dissecta</i> Lesquereux			Colorado		
8. <i>A. (?) gracilis</i> Lesquereux		Wyoming			
9. <i>A. hercules</i> (Unger) Saporta	Colorado				
10. <i>A. jorgensenii</i> Heer	Greenland	Mississippi			
11. <i>A. lasseniana</i> Lesquereux		California			
12. <i>A. lobata</i> Knowlton	Colorado				
13. <i>A. longipetiolata</i> Jennings			Montana		
14. <i>A. looziana</i> Saporta & Marion	Montana				
15. <i>A. notata</i> Lesquereux	Montana Colorado Wyoming North Dakota Alberta Saskatchewan	British Columbia Oregon Arkansas Louisiana Texas			
16. <i>A. notata denticulata</i> Berry		Wyoming			
17. <i>A. reesidei</i> Knowlton	Colorado				
18. <i>A. republicensis</i> Brown				Washington	
19. <i>A. rubyensis</i> Becker				Montana	
20. <i>A. (?) semina</i> Berry		Kentucky			
21. <i>A. (?) serrata</i> Knowlton	Colorado New Mexico				
22. <i>A. serrulata</i> Knowlton	Wyoming				

Table 1. Cenozoic ARALIACEAE AND UMBELLIFERAE of North America (Continued)

	Paleocene	Eocene	Oligocene	Miocene	Pleistocene
23. <i>A. taurinensis</i> (Ward) Sanborn	Montana Saskatchewan Alberta	Oregon Louisiana Kentucky Texas			
24. <i>A. triloba</i> Newberry	North Dakota Saskatchewan				
25. <i>A. wrightii</i> Knowlton				Wyoming	
26. <i>A. wyomingensis</i> Knowlton & Cockerell	Wyoming Colorado				
27. <i>A. (?)</i> sp. Hollick		Alaska			
28. <i>A. (?)</i> sp. Hollick		Alaska			
29. <i>A.</i> sp. Knowlton				Wyoming	
30. <i>A.</i> sp. Knowlton		Oregon			
31. <i>A. (?)</i> sp. Knowlton		Oregon			
32. <i>A. (?)</i> sp. Knowlton	Colorado				
33. <i>A.</i> sp. Lesquereux		Louisiana			
34. <i>Aralinium excellens</i> Platen		California			
35. <i>A. lindgreni</i> Platen		California			
36. <i>A. multiradiatum</i> Platen		California			
37. <i>A. parenchymaticum</i> Platen		California			
38. <i>Panax andrewsii</i> Cockerell			Colorado		
ARALIACEAE-SCHEFFLERAE					
1. <i>Hedera auriculata</i> Heer		Alaska			
2. <i>H. parvula</i> Ward	Montana				
3. <i>Oreopanax conditi</i> La Motte			Nevada		
4. <i>O. gigantea</i> (Knowlton) Arnold				Oregon Mississippi	
5. <i>O. minor</i> Berry		Tennessee			
6. <i>O. mississippiensis</i> Berry		Mississippi			
7. <i>O. oxfordensis</i> Berry		Arkansas Mississippi			
8. <i>O. precoccinea</i> (Brooks) Arnold				Oregon Idaho	
9. <i>O. wilcoxensis</i> Berry		Tennessee Texas			
10. <i>O. wilcoxensis crenulatus</i> Berry		Tennessee			
11. <i>O. (?)</i> sp. Bell	Alberta				
12. <i>Schefflera elliptica</i> Berry		Tennessee Kentucky			
13. <i>S. formosa</i> Berry		Tennessee Kentucky			
UMBELLIFERAE-APIOIDEAE					
1. <i>Cymopterus</i> (<i>Glehnia</i>) <i>littoralis</i> Gray					California
2. <i>Daucus pusillus</i> Michx.					California
3. <i>Oenanthe sarmentosa</i> Presl					California
4. <i>Oxypolis destructus</i> Cockerell			Colorado		
5. <i>Peucedanites nordenskiöldi</i> Heer	Greenland				
6. <i>Umbellifercspermum lata-</i> <i>hense</i> Berry				Washington	
7. <i>Zizia</i> sp. Brown					Louisiana

¹ Taken from Boureau, 1965-64; Knowlton, 1919; La Motte, 1944, 1952. No records for Pliocene.

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